THE UNIVERSITY OF CHICAGO

THE EFFECTS OF BRAIN INJURY UPON RETENTIVENESS IN THE RAT

A DISSERTATION SUBMITTED TO THE FACULTY OF THE DIVISION OF THE BIOLOGICAL SCIENCES IN CANDIDACY FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF PSYCHOLOGY

1934

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THE EFFECTS OF BRAIN INJURY UPON RETENTIVENESS IN THE RAT*[1]

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I. STATEMENT OF THE PROBLEM

The problem of learning resolves itself into two aspects: the act of acquisition and that of retention. Living organisms not only show modifications of behavior after repeated stimulations, but retain traces of the modification. It is a universally recognized fact that as time goes by retained traces of formerly learned activities gradually fade away. In human psychology, Ebbinghaus has made the first systematic attempt at a quantitative study of memory and objective measurement of factors governing fixation, retention, and recall in verbal learning (4). By memorizing lists of nonsense syllables and recalling them afterwards he was able to ascertain in numerical terms the definite amount retained or obliterated after a lapse of a longer or shorter period. Thus in quantitative measures, Ebbinghaus established forgetting as a function of the time elapsed between learning and recall.

The work of Müller and Pilzecker introduced another methodological approach to the subject (22). They interpolated various activities between initial learning and later relearning of nonsense materials and discovered that the second activity exerted a deleterious influence upon the retention of the original material. To this influence they applied the term "retroactive inhibition" (*rückwirkende Hemmung*). They argued, therefore, that forgetting is not only a function of the time alone as Ebbinghaus has claimed, but also a function of the interpolated activity between learning and recall.

The neurological implications of the function of retention and

*Recommended for publication by K. S. Lashley, and received in the Editorial Office on October 15, 1937.

[1]This study was carried out in the Psychological Laboratories of the University of Chicago under the kind direction of Prof. K. S. Lashley, to whom I wish to express my deep indebtedness. Thanks are also due to my beloved wife for assistance in preparation of the manuscript.

of forgetting are by no means clear. Psychologists, following traditional custom, postulate specific connections of memory traces within the central nervous system. A repeated stimulus calls forth a more or less definite reaction with a specifically intercalated "engram" in between. The pattern of the engrams or memory traces remains relatively permanent as repeated stimulations cause a greater and greater reduction of resistance in the synaptic connections. This altered synaptic condition, they claim, explains the fact of memorization and habit formation. Forgetting, on the other hand, is attributed to the weakening of bond connections through disuse.

An interesting experiment on the process of forgetting during sleep and waking hours was performed by Jenkins and Dallenbach (9). A comparison was made between the rate of forgetting after 1, 2, 4, and 8 hours of sleep or waking after learning a constant series of nonsense syllables in two subjects. The data indicated a marked difference in the rate of forgetting during sleep as compared with waking. On the average, more than twice as many syllables were reproduced by both subjects after intervals of sleep than after intervals of waking. This is highly significant, as in the sleep condition "retroactive" influences are presumably reduced to a minimum. The authors suggested that "forgetting is not so much a matter of the decay of old impressions and associations as it is a matter of the interference, inhibition, or obliteration of the old by the new" (9, p. 612). On the basis of this result as well as of data on the so-called retroactive inhibition, McGeoch formulated the hypothesis that the positive interference of memory traces from interpolated activities instead of the negative condition of disuse is the major contributing factor of forgetting (19).

Lashley's fundamental experiments on the cerebral functions in learning and retention in rats have revealed some of the most illuminating data relative to the neural mechanisms underlying the processes of retention and forgetting. In a series of experiments, he demonstrated that post-training brain lesions produce a definite amnesia of certain sensori-motor habits the degree of which is directly proportional to the extent of the tissue injured but is independent of the locus of the lesion (11). He further reported a greater loss of maze habits in animals with cerebral lesions preceding initial training than in normal animals. He ascribed this to a defect in retentiveness due to the loss of cerebral tissue (12). Such facts

tend to show that memory traces are weakened not only by the mere passage of time (Ebbinghaus), nor by the additional factor of interpolated activity between learning and retention (Müller and Pilzecker), but they are weakened also by the existence of a cerebral lesion. These experimental results are of considerable importance for the interpretation of neural organization in habit. Lashley used his results as evidence against the existence of specific bonds or connections in the memory trace, arguing that the absence of some remote part of the cortex should not affect the permanence of well-established connections if they were local in character, and that the reduced retentiveness must be taken as evidence for some non-localized function of the whole cortex in retention.

Lashley's interpretation was questioned, however, by Melton, who pointed out that in the interval between learning and retention tests for the maze, Lashley trained the animals in a number of other problems, and that therefore the factor of so-called retroactive inhibition must be taken into account (16). Melton assumed that such inhibition might be more effective in disrupting the habits of animals deteriorated as a result of cerebral lesion and that greater susceptibility to "retroactive inhibition" rather than reduced retentiveness might be responsible for the results. If Melton's argument is substantiated, it will lend support to the theory of specific connections, at least by weakening the evidence against the theory. It was the purpose of the present experiments to test the relative effectiveness of training interpolated between learning and retention tests in producing a loss of memory for the maze habit in normal animals and in animals with more or less extensive cerebral lesions. Only by a systematic control of the factors of time, interpolated activity, as well as cerebral lesions, we believe, could we hope to bring to light some of the basic processes, neurological or otherwise, underlying the function of retention or forgetting. (The fallacy of the concept of so-called retroactive inhibition has been pointed out in a critical review of literature bearing on the problem to be published elsewhere. For this reason, the author refuses to adopt the term "retroactive inhibition" in the present report.)

II. General Plan of the Experiments

The problem of the present study consists in determining the presence and amount of the disruptive influence, if any, caused by

an interpolated second maze activity upon the retention of a first maze in two groups of rats with and without cerebral lesions. The interval between learning and retest of the first habit remains constant in both cases. Two other groups of normal and operated animals under parallel conditions but without training on the interpolated maze are used as controls. The general organization of the

TABLE 1

PLAN OF THE ORGANIZATION OF THE EXPERIMENTS

Group	No. of cases	Procedure
Norm. I—without interpolated learning	25	40 days Learn Maze A—no learning—Relearn Maze A
Norm. II—with interpolated learning	25	40 days Learn Maze A—learn Maze B—Relearn Maze A
Oper. I—without interpolated learning	23	40 days Learn Maze A—no learning—Relearn Maze A
Oper. II—with interpolated learning	22	40 days Learn Maze A—learn Maze B—Relearn Maze A

experiments is roughly represented in Table 1. The following four groups of animals were trained:

1. Normal Group I. This group was trained on Maze *A* (Fig. 1) and after mastery was allowed forty days without training during which the animals traversed once daily a straight runway (Fig. 3) and were fed at the usual experimental hour. At the expiration of the 40-day interval, Maze *A* was relearned by this group of subjects.

2. Normal Group II. This group went through the same procedure as the above group with the exception that after mastery of Maze *A* the rats were given a rest period of 7 days and were fed at the end of the runway. On the eighth day the animals were transferred to Maze *B* (Fig. 2) for training until mastery. The interval between the completion of learning of Maze *A* and its relearning was always 40 days. In cases where Maze *B* was learned before the termination of the 40-day period, the rats were fed daily in the runway thereafter up to the 41st day on which relearning of Maze *A* started.

3. Operated Group I. The procedure of Normal Group I was exactly duplicated on rats with different amounts of cerebral lesions.

4. Operated Group II. This group was trained under parallel conditions as Normal Group II excepting that the animals in this group were operated before training.

Description of the Mazes.

Maze *A* was adopted for original learning. This was an 8 culs-de-sac maze with alternate left and right turns for the correct path. The original maze described by Lashley and Wiley (15) was used. Errors were recorded by personal observation.

To guarantee accuracy in recording of some operated cases which made hundreds of errors in a single trial, the errors were accumulatively tabulated on a sheet of paper according to the usual statistical tabulation technique in groups of 5 tallies.

The ground plan of the maze is shown in Figure 1. The reliability

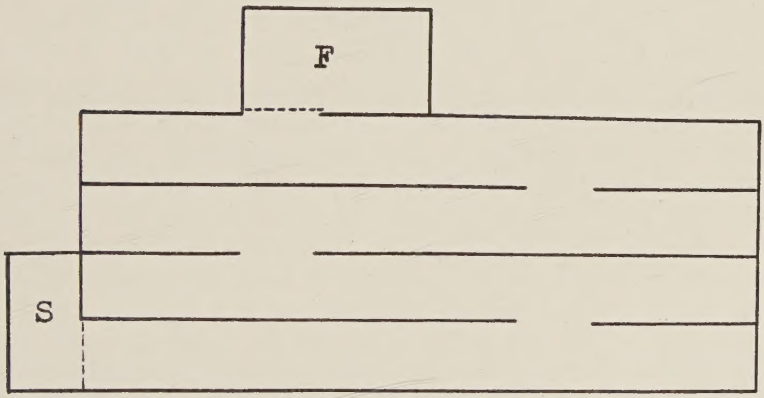

FIGURE 1
MAZE A

of the maze as a measurement of the function of learning and retention has been adequately dealt with by Lashley (12) and Lashley and Wiley (15). The maze gives a reliable measure of individual variations of the magnitude occurring among animals with cerebral lesions. For interpolated learning, Maze *B* (Figure 2) was used, which is one of the Carr mazes. It is a square maze containing 12

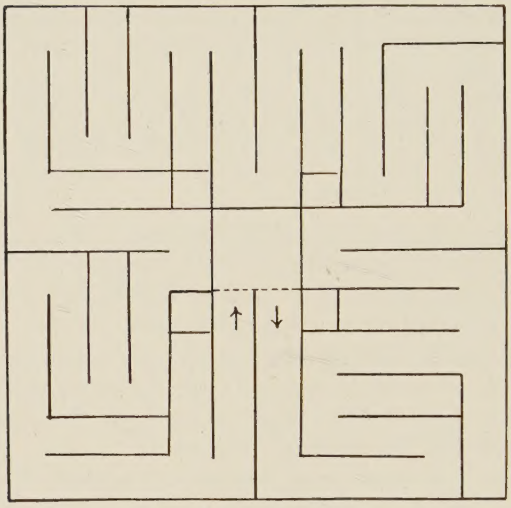

FIGURE 2
MAZE B

culs-de-sac, and is the same one which Pechstein used for whole and part learning (23). The choice of this maze for interpolated material is purely an arbitrary one. The reliability of this maze is undetermined. Judged by Pechstein's records as well as by mine, this maze is a comparatively easier one to master than Maze *A*, but is sufficiently dissimilar in pattern relationship from the latter to demand an entirely new orientation in learning it. One normal rat that developed a position habit and two more seriously deteriorated operated animals failed to master the problem during the interpolated period. In contrast to this, four cases of the same group failed entirely to relearn Maze *A*. Figure 3 represents a straight runway 10 feet in length with a food box at one end. It was used

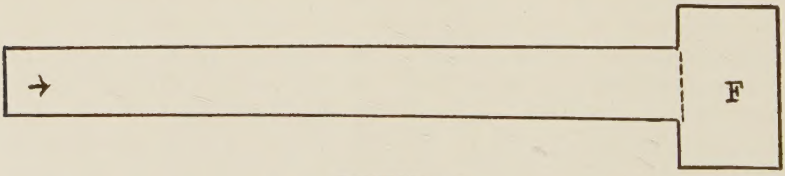

FIGURE 3
A STRAIGHT RUNWAY

to give the animals some exercise and habituation to handling during the retention period.

Criteria of Learning.

As criterion of learning a rigid record of 10 consecutive errorless trials was taken, but training was discontinued in case the animal failed to reach criterion after 150 trials, after which the animal was launched immediately into the next stage of the experimental procedure. So to each of the most serious cases of operated animals which failed entirely to reach the criterion, a maximum of 102 days was devoted, 31 days for original learning, 40 for interpolation and another 31 days for relearning.

Of the different criteria of learning used in these experiments errors are probably the most reliable. The reliability of total trials is lessened by the fact that a casual making of one error before completion of an individual record would disproportionately add 10 more trials to the total whereas the error score gives only one more. Moreover, all those cases which failed to reach criterion in learning 150 trials after the initial trial were discontinued and hence an equal weight was given to all of them in terms of total trials. Nevertheless, their learning records could still be differentiated when measured by total errors. To partially correct this, figures are computed by subtracting from the total trials the number of errorless trials. Time scores were not used on account of their questionable reliability, especially in the case of operated animals.

Reliability of the Mazes.

There are several ways of determining the reliability of the maze as an instrument for measuring the consistency of performance in rats. One of them is to correlate the learning with relearning scores on the same maze, and another method is by comparing the learning scores made in two or more different mazes. Lashley finds a markedly high correlation for animals with different amounts of cerebral lesions and suggests this as a further criterion for the reliability of the maze. We have computed in Table 2 the correlation coefficients of learning with relearning scores for both normal and operated groups by the rank difference method. An inspection of the table shows that the correlations between learning and relearning on Maze *A* in both normal groups are low, of the order of 0.34 in

TABLE 2

CORRELATION BETWEEN LEARNING AND RELEARNING OF MAZE *A* FOR NORMAL AND OPERATED GROUPS AS MEASURED BY THE RANK DIFFERENCE METHOD

Group	Errors	Trials	Trials Minus Correct Runs
Norm. I	0.34±0.13	—0.03±0.14	—0.42±0.12
Norm. II	0.32±0.13	0.12±0.14	0.16±0.14
Oper. I	0.62±0.12	0.35±0.13	0.49±0.11
Oper. II	0.86±0.04	0.58±0.09	0.71±0.07

the case of Group I and 0.32 in Group II. On the other hand, the correlation between learning and relearning in Operated Group I is of the order of 0.62±0.12, and that of the interpolative group is even higher, of the order of 0.86±0.04 in terms of errors. This markedly higher correlation in Group II may be either accountable by the wider distribution of the amount of tissue destroyed in the group (*vide infra*) or that the interpolated activity tends to enhance the correlation value between learning and relearning.

Table 3 shows the inter-maze correlations between the original

TABLE 3

INTER-MAZE CORRELATIONS FOR THE NORMAL AND OPERATED INTERPOLATIVE GROUPS IN TERMS OF ERRORS AND TRIALS

		Norm Gr. II	Oper. Gr. II
Maze A Learning with	Errors	0.51±0.10	0.83±0.05
Maze B Learning	Trials	0.32±0.13	0.60±0.09
Maze A Relearning	Errors	0.23±0.13	0.79±0.06
with Maze B Relearning	Trials	0.14±0.14	0.69±0.08

Maze *A* and the interpolated Maze *B* for both normal and operated groups of animals. Correlation of learning score on Maze *A* with that on Maze *B* gives 0.51±0.10 for the normal group and 0.83±0.05 for the operated cases in terms of errors. Comparison of relearning scores on Maze *A* with learning scores on Maze *B* gives similar though less marked relationship. Correlation values for the operated groups are always significantly higher than those of the normals. All the figures indicate that those operated animals which made low records in learning Maze *A* tend also to make low records in relearning the same maze as well as in learning a different maze, and supports Lashley's contention that the maze

is a reliable measure for the function of learning and retention in animals with cerebral lesions although it is somewhat questionable as such in the case of normals.

Selection of Animals, Motivation and Scoring Methods.

The animals used in the experiments were taken from a stock colony raised in the laboratory. This is a strain derived from a cross of Wistar stock with trapped wild rats. None of them had any experience in mazes prior to the experiment. With one exception in the operated group, the animals were all males. They ranged in age from 4 to 5 months at the beginning of the experiment. Animals from the general colony were distributed at random in the control and operated groups, which were roughly equated with respect to maturity and weight. Siblings were not used. Both operated and normal animals were given preliminary training in the straight runway to adapt them to handling. This was continued until the animals went promptly to the food and showed no disturbance when handled.

A total of 53 normal rats was trained, but three died during training, leaving 50 which completed the series, 25 in each group. The mortality rate of the operated animals was much higher than that of the normals. From a total of 56 operated rats 8 were lost. Of the remaining 48, one was discarded because of infection revealed at necropsy, and one brain was accidentally destroyed. One animal with a severe lesion made so many errors during initial training (three times the maximum of any other animal) that it was judged atypical and its record excluded. This left 23 complete records for Group I, without interpolated learning, and 22 for Group II, with interpolated activity.

All the animals were motivated in learning by 24-hour hunger, but they were deprived of food the day before being put into the maze when original learning, interpolated learning or relearning was first begun. In the first day of training, one trial was given and five trials per day thereafter. This was true both in original learning and in relearning on Maze *A*. Five trials each day were given throughout the interpolated learning of Maze *B*. After each trial the animal was allowed a nibble of food in the food box and the next trial was immediately started. At the completion of five trials the rat was fed in the food box for about 10 minutes or to repletion.

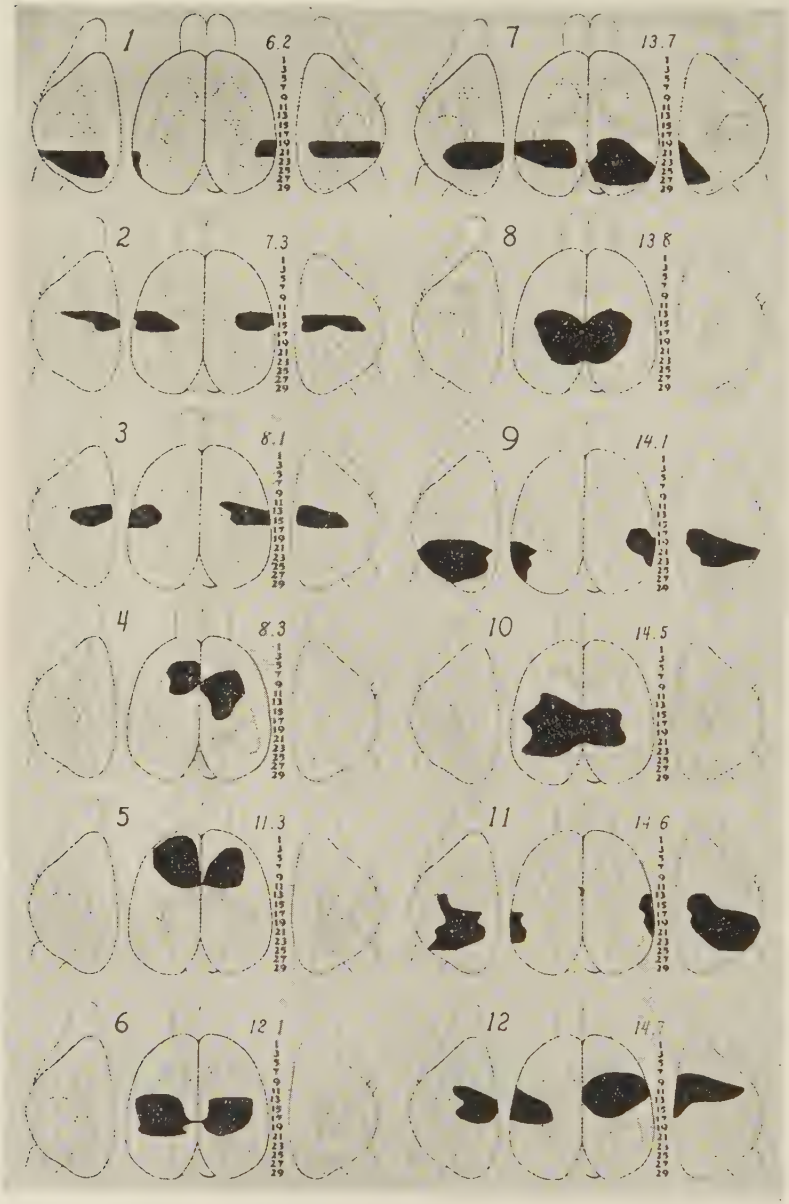

FIGURE 4 a
GROUP I

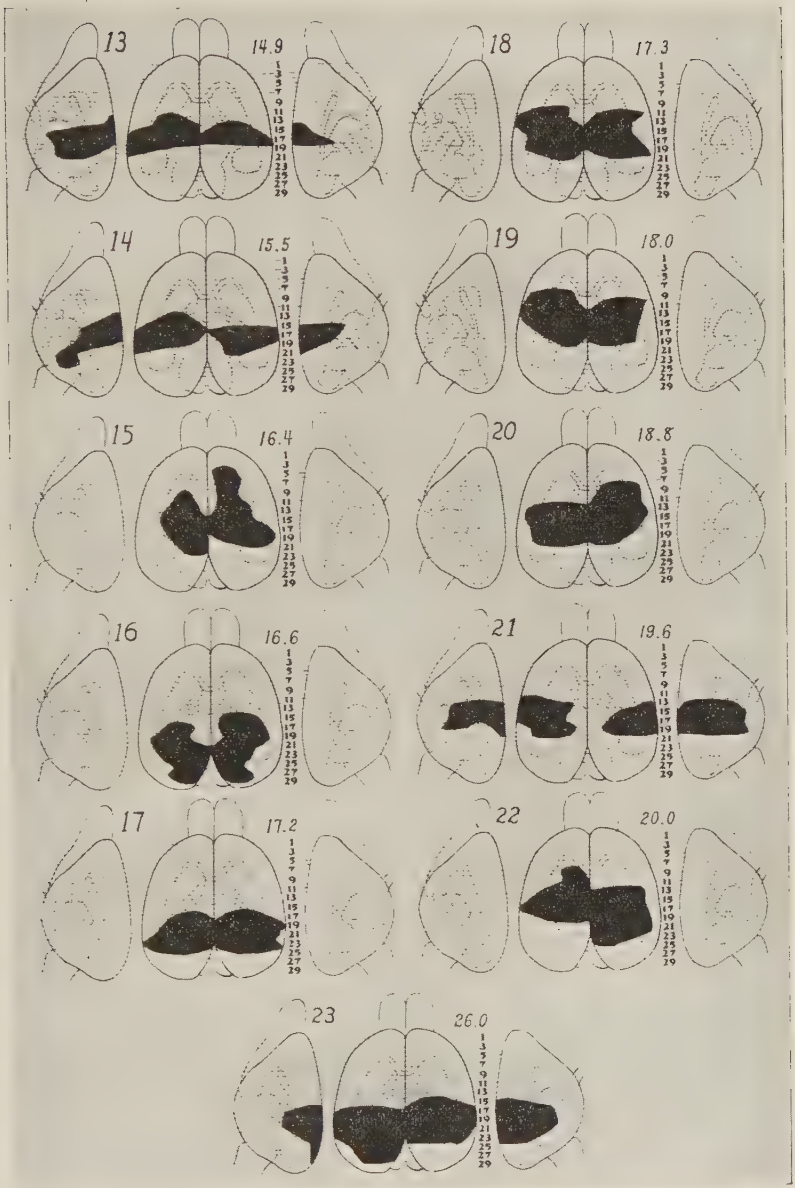

FIGURE 4 b
GROUP I (continued)

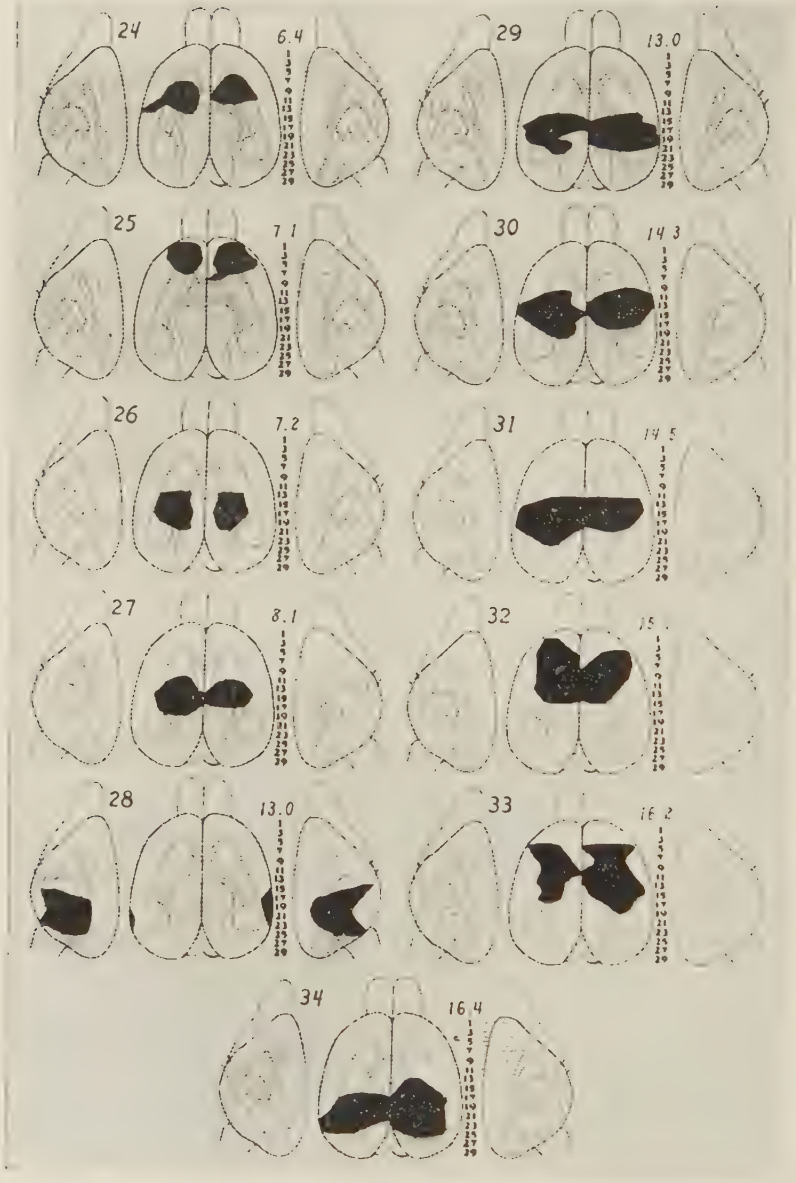

FIGURE 5 a
GROUP II

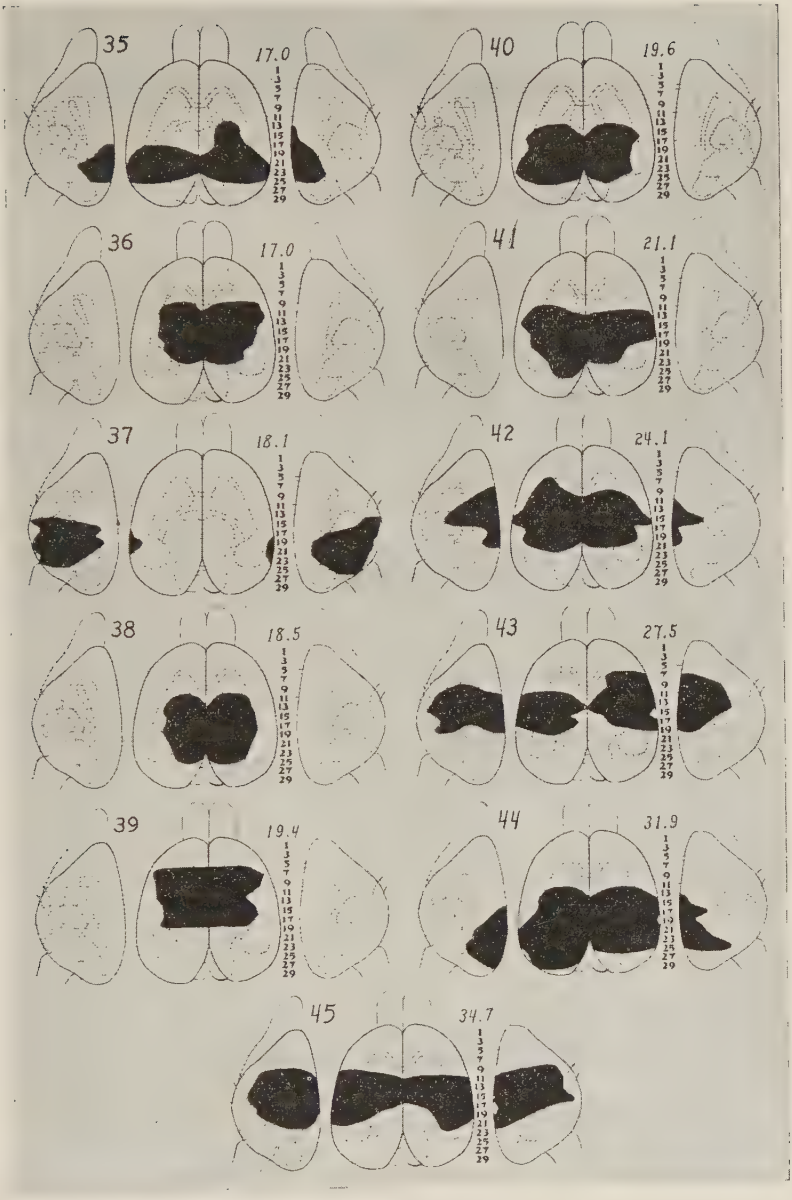

FIGURE 5 b
GROUP II (continued)

To ensure strict adherence to the exact number of days during which the subjects should be trained or otherwise treated as prescribed under different conditions, a collective record sheet in terms of total errors per day was provided. The days during the retention period with or without interpolated learning were marked with a red or blue pencil respectively so that the exact number of days elapsed could always be told at a glance.

Operative Techniques and Special Methods.

The details of operative techniques have been amply described by Lashley (12, pp. 16 ff.). For the present only a brief description is necessary. Operations were performed with thermocautery under ether anesthesia with aseptic precautions. The lesions were made as symmetrical as possible in the two cerebral hemispheres and covered diverse areas in different animals. Most of the animals recovered very rapidly after operation and a period of 10 days was allowed for recuperation. As far as possible the operated animals were run in the straight pathway (Figure 3) during the interval so as to get adapted to handling. From the seventh day the rats were fed in the food compartment of Maze *A* without access to the other parts of the maze in order to acquire some habituation before training, which usually began 10 days after the date of operation. In some cases in which there were severe lesions or which showed paretic involvements or other physical weaknesses, extra time ranging from a few days to a couple of weeks was allowed for recovery. Objections may be raised as a prolongation of the pretraining period would introduce an age factor into both learning and retention situations, but as such cases were rare the difference is negligible. In the case of normal animals the pretraining period for acquaintance with the food box and adaptation to handling usually covered three or five days. After the operated animals had completed the series their brains were taken out and the position and extent of the superficial lesions roughly sketched on a printed diagram (Figures 4-5). The brains were fixed, sectioned and stained with thionin. For the details of the graphic method of serial reconstruction and planimetric measurement of the percentages of areas of lesions, the reader is referred to Lashley's reports.

TABLE 4

INDIVIDUAL LEARNING AND RELEARNING SCORES OF THE NORMAL GROUPS ON MAZE *A* BY ALL MEASURES WITH INTERPOLATED LEARNING SCORES ON MAZE *B* INCLUDED

Group I (Without interpolated learning)									Group II (With interpolated learning)											
	Learning				Relearning					Learning			Relearning				Interpolated learning		
Serial No.	Errors initial trial	Total errors	Total trials	Trials less correct runs	Errors initial trial	Total errors	Total trials	Trials less correct runs	Serial No.	Errors initial trial	Total errors	Total trials	Trials less correct runs	Errors initial trial	Total errors	Total trials	Trials less correct runs	Total errors	Total trials	Trials less correct runs
1	9	59	51	20	0	1	12	1	26	4	74	60	25	0	27	76	16	33	35	11
2	9	24	80	38	0	0	14	2	27	4	45	57	24	4	5	16	2	24	22	9
3	15	112	39	12	0	3	11	1	28	13	48	26	13	4	8	13	3	14	27	8
4	9	35	40	9	1	1	10	0	29	4	52	34	15	0	5	26	4	28	14	4
5	37	71	18	8	0	6	24	5	30	10	30	31	8	1	2	15	2	19	14	4
6	15	65	30	17	1	1	11	1	31	6	19	19	6	0	1	18	1	24	22	10
7	3	70	38	23	2	6	17	3	32	13	54	37	10	1	3	20	2	52	40	19
8	6	88	65	34	0	6	20	3	33	25	97	50	22	1	1	11	1	51	29	11
9	8	69	86	31	0	11	50	10	34	5	42	36	15	3	9	26	4	23	23	5
10	3	24	26	11	1	4	21	4	35	15	41	29	13	0	4	20	3	36	25	13
11	23	197	44	24	0	6	29	4	36	10	20	29	10	0	12	26	4	22	21	6
12	21	38	33	12	0	5	36	3	37	34	72	40	15	1	14	59	14	29	22	10
13	11	46	44	17	0	0	10	0	38	5	81	120	42	0	5	25	5	17	26	9
14	34	100	28	15	0	4	29	3	39	22	203	77	38	13	13	11	1	159	103	44
15	25	78	44	13	1	13	66	10	40	31	114	60	33	0	13	28	6	58	73	23
16	13	74	50	23	0	4	26	3	41	13	39	65	18	0	0	10	0	11	13	3
17	4	80	34	18	3	3	11	1	42	44	111	71	31	1	2	21	2	39	32	6
18	11	30	25	11	0	11	32	7	43	5	90	69	34	0	2	24	2	19	29	8
19	12	64	56	26	1	2	19	2	44	12	136	76	34	2	29	106	24	108+	160	63
20	17	116	93	42	1	6	34	5	45	9	95	53	22	4	13	31	7	40	60	24
21	35	76	30	14	0	1	15	1	46	46	112	33	18	0	0	10	0	33	37	23
22	11	104	104	51	1	1	11	1	47	21	67	23	10	1	6	26	4	142	84	33
23	28	59	65	19	0	0	10	0	48	49	69	38	11	1	2	16	2	33	64	19
24	16	44	28	11	0	0	10	0	49	5	46	38	15	0	3	18	1	37	32	13
25	7	76	79	27	0	1	16	1	50	4	39	65	22	0	1	16	1	63	103	36
To.	382	1799	1230	526	12	96	544	71		409	1796	1230	504	37	180	688	111	1114	1110	414

+ denotes cases which failed to reach criterion during the allotted interval.

TABLE 5

AVERAGES OF LEARNING SCORES ON MAZE *A* FOR THE FOUR GROUPS OF ANIMALS USED IN THE EXPERIMENT

Group	No. of animal	Average percent lesion	σdis.	Errors	σdis.	Errors first trial	σdis.	Trials	σdis.	Trials minus errorless runs	σdis.
Norm. I (Without interpolation)	25	0	—	71.96±4.83	35.83	15.28±2.8	20.75	49.2±3.17	23.51	21.04±1.48	10.98
Norm. II (With interpolation)	25	0	—	71.84±5.58	41.4	16.36±1.84	13.61	49.2±3.19	23.68	20.16±1.26	9.35
Oper. I (Without interpolation)	23	14.74±0.71	5.08	279.65±50.14	356.51	20.87±4.24	30.19	95.82±5.81	41.30	56.74±7.86	55.88
Oper. II (Without interpolation)	22	17.28±1.02	7.09	277.86±32.56	226.38	26.77±3.76	26.21	100.4±2.04	14.18	65.73±6.29	43.75

III. Analysis of Experimental Data

1. *Comparison of the Normal Groups.*

The individual learning and relearning scores of the two normal groups on Maze *A* together with learning scores on the interpolated Maze *B* by all measures are summarized in Table 4. The averages of learning scores of the groups compared on Maze *A* are given in Table 5, and Table 6 shows the average relearning scores in all measures.

A. Equation of groups in initial learning ability. It is to be remembered that the two groups were all taken from the same stock, were of about equal age, all of the same sex, and were trained in identical situation. They should represent equally normal distributions and about the same level of learning ability in the maze. This is all the more strengthened by a comparison of the average learning scores of the two groups on Maze *A* (Table 5). The two groups made practically equal number of errors in learning the maze (71.96 ± 4.83 for Group I vs. 71.84 ± 5.58 for Group II), and the numbers of trials were exactly identical in the two cases, which is of course a matter of happy chance (49.2 ± 3.17 of Group I as against 49.2 ± 3.19 of Group II), but the number of total trials minus correct runs for Group I (21.04 ± 1.48) and for Group II (20.16 ± 1.26) tells practically the same story. On the basis of these figures we may safely conclude that the two groups started out with closely equal levels of learning proficiency on Maze *A*.

B. A comparison of relearning scores. In marked contrast to the almost exact equality of initial learning scores, the two groups show a significant difference in relearning values. Figures in Table 6 indicate that Group I made an average relearning score of 3.84 ± 0.47 errors whereas Group II made a much higher average record of 7.2 ± 0.98. The difference (3.36 ± 1.09) is three times its probable error and, although small in terms of absolute figures, is reliable evidence of a deleterious effect of the interpolated activity which caused almost twice as many errors in the relearning of the test group as those of the controls. Figures for average trials minus errorless runs show a similar though less marked trend: the averages for the interpolated and for the non-interpolated groups being 4.44 ± 0.76 and 2.84 ± 0.37 respectively, with a difference of 1.6 ± 0.84. In terms of trials, however, Group I required an average of 21.76 as

TABLE 6

AVERAGES OF RELEARNING SCORES ON MAZE *A* FOR THE FOUR GROUPS OF ANIMALS USED IN THE EXPERIMENT

Group	No. of animal	Percent lesion	σdis.	Errors	σdis.	Errors first trial	σdis.	Trials	σdis.	Trial minus errorless runs	σdis.
Norm. I (Without interpolation)	25	0	—	3.84±0.47	3.5	0.28±0.1	0.75	21.76±1.81	13.4	2.84±0.37	2.74
Norm. II With interpolation)	25	0	—	7.2±0.98	7.23	1.48±0.36	2.71	26.72±2.81	20.83	4.44±0.76	5.64
Difference				3.36±1.09		1.2±0.36		4.96±3.34		1.6±0.84	
Oper. I (Without interpolation)	23	14.74±0.71	5.08	27.32±6.34* (63.74±36.36)	44.09* (174.4)	1.91±0.27* (3.65±1.18)	1.86* (8.37)	49.61±6.15	43.73	20.83±4.92	34.97
Oper. II (With interpolation)	22	17.28±1.02	7.09	66.38±12.53 (104.18±27.17)	91.89* (188.9)	3.23±0.44	3.06	61.59±8.05	55.97	33.36±6.49	45.14
Difference		2.54±1.24		39.06±13.04		1.32±0.52		11.98±10.13		12.53±8.14	

*Constants are computed by omitting one case whose score exceeds 40xσdis. Figures in brackets represent uncorrected values. Records for trials are unaffected.

against the 26.72 of Group II in relearning the same maze. The difference is not reliable. Summarizing all the values together, we may conclude that there is a significant inferiority in retention of the interpolative group as contrasted with the one without interpolated activity.

C. Comparison of errors made in the first trial of learning and relearning tests. Our experimental procedure makes a direct comparison of the error scores in the first trial of learning and relearning tests possible, as the animals were given only one trial on the first day when learning or relearning began (see Tables 4-6). For original learning Group I made an average of 15.28 ± 2.8 errors and Group II made a score of 16.36 ± 1.84 in the initial trial. Here the two figures are very close. The relearning values show an average of 0.28 ± 0.1 in the case of Group I and 1.48 ± 0.36 in the case of Group II which made roughly five times as many initial errors as the former, the difference being 1.2 ± 0.36. In Group II one rat (No. 39) made a gross error score of 13, which far exceeds any of the others. When this case is excluded, however, the interpolative group still made twice as many errors in the first trial of relearning tests as the control group.

D. Individuals unaffected by time or interpolated activity during retention. In Group I, 16 animals made perfect scores in the initial trial of relearning; in Group II, 12 rats showed no disintegration of the old habit in the initial trial. Four rats of Group I and only two of Group II made perfect scores throughout the relearning period. This is in agreement with the other evidence for the better retention of the group without interpolated training.

E. Summaries of results relative to the two normal groups.

1. With the initial learning efficiencies of the two normal groups almost exactly equated in error and trial scores, the group (Group II) that relearned the maze 40 days after mastery, during which the animals were engaged in learning another different maze, made almost twice as many errors in relearning as the group without interpolated learning. The excess in terms of trials is roughly one-fourth and about three-fifth in terms of total trials minus errorless runs.

2. A comparison of the errors made in the first trial of relearning of the two groups as well as the number of individuals which showed perfect retention scores further supports the conclusion that

TABLE 7

INDIVIDUAL LEARNING AND RELEARNING SCORES OF THE TWO OPERATED GROUPS ON MAZE *A* BY ALL MEASURES WITH INTERPOLATED LEARNING SCORES ON MAZE *B* INCLUDED

Group I (Without interpolated learning)											Group II (With interpolated learning)											
		Learning				Relearning						Learning				Relearning				Interpolated learning		
Serial No.	Percent lesion	Errors initial trial	Total errors	Total trials	Trials less correct runs	Errors initial trial	Total errors	Total trials	Trials less correct runs	Serial No.	Percent lesion	Errors initial trial	Total errors	Total trials	Trials less correct runs	Errors initial trial	Total errors	Total trials	Trials less correct runs	Total errors	Total trials	Trials less correct runs
1	6.2	75	128	49	27	0	6	28	5	24	6.4	7	129	57	38	8	36	47	13	88	160	64
2	7.3	12	70	55	28	2	6	19	3	25	7.1	5	54	79	27	0	1	13	1	18	17	6
3	8.1	9	100	114	47	4	5	12	2	26	7.2	12	41	35	16	1	1	11	1	15	31	8
4	8.3	7	257+	151	61	1	9	26	6	27	8.1	6	441	125	58	8	36	23	6	241+	59	45
5	11.3	8	58	46	29	1	8	29	7	28	13	11	43	30	9	2	3	14	2	29	32	11
6	12.1	14	257	92	53	0	7	41	7	29	13	5	86	64	33	2	6	15	4	103	95	52
7	13.7	131	1495+	151	151	42	865+	151	151	30	14.3	10	70	72	38	0	0	10	0	62	36	26
8	13.8	63	1109+	151	131	6	173	121	69	31	14.5	51	251+	151	92	3	21	30	9	92	62	24
9	14.1	7	132	74	44	4	47	79	26	32	15.1	13	113	135	50	1	9	31	6	77	74	37
10	14.5	6	86	74	41	3	63	96	34	33	16.2	11	302+	151	120	2	110+	151	73	108	90	54
11	14.6	19	70	39	15	0	1	15	1	34	16.4	20	100	57	31	1	17	45	11	62	53	27
12	14.7	13	43	48	16	1	3	16	2	35	17	4	111	123	46	0	4	24	2	49	53	20
13	14.9	5	183	85	50	2	20	70	17	36	17	51	163	62	39	4	11	26	6	50	61	27
14	15.5	8	134	91	38	0	16	53	11	37	18.1	55	104	44	19	3	55	115	36	75	45	15
15	16.4	4	198+	151	84	2	41	74	25	38	18.5	104	544+	151	107	6	110	19	9	138	83	32
16	16.6	17	265+	151	119	2	146+	151	82	39	19.4	20	617+	151	151	4	190+	151	101	126	141	76
17	17.2	16	164	87	55	0	7	30	6	40	19.6	25	144	66	40	3	9	28	7	73	45	25
18	17.3	4	102	106	45	0	1	13	1	41	21.1	21	254	111	68	2	15	48	8	100	51	26
19	18	3	59	63	32	1	4	19	4	42	24.1	52	790+	151	151	3	306	101	101	176	180	98
20	18.8	16	169	146	72	0	8	32	5	43	27.5	17	1047+	151	136	1	346+	151	124	381+	200	173
21	19.6	5	96	50	29	3	13	33	9	44	31.9	6	136	92	59	4	108	151	64	167	160	111
22	20	25	256+	151	85	5	8	18	3	45	34.7	23	573+	151	118	13	898+	151	150	97	122	59
23	26	13	641	79	53	5	9	15	3													
Total	339	480	6432	2204	1305	84	1466	1141	479		380.2	589	6113	2209	1446	71	2292	1355	734	2327	1850	1016

\+ Denotes cases which failed to reach criterion during the allotted interval.

the retention values of the interpolative group are inferior to those of the non-interpolative group.

2. *A Comparison of the Operated Groups.*

A. Equation of the groups in average percentage of lesions and in initial learning ability. The percentage of the cortical area destroyed in any animal is largely a chance affair. It has turned out that the average percent of lesion in Group I is 14.74 ± 0.71 with a $\sigma dis.$ of 5.08, and that of Group II is 17.28 ± 1.02 with a $\sigma dis.$ of 7.09 (Tables 5-6). Group II has evidently a slightly greater average percentage of cerebral injury and a wider scatter in distribution. Nevertheless, the average learning scores for Group I are errors = 279; trials = 95.82; and trials minus errorless runs = 56.74; and for Group II: errors = 277; trials = 100.4; and trials less correct runs = 65.73. As the difference is in no case statistically reliable, we may say that the two groups made practically equal scores in initial learning performances (Table 7).

B. A comparison of the relearning scores of the operated groups. When a comparison was made of the relearning scores of the two operated groups, the score of one animal in each group was found to exceed four times the standard deviation of the group. It is questionable whether such wide deviates from the norm of the group may be legitimately included in the computation of constants. The chief constants have therefore been computed both including and excluding these two cases. In Table 6 the averages marked with an asterisk are corrected by the exclusion of the two cases. These corrected constants are used in later discussions.

In terms of errors, Group I made an average relearning score of 27.32 ± 6.34 as compared with 66.38 ± 12.53 of Group II, the difference being 39.06 ± 13.04 in favor of the former. Group I required an average of 49.61 ± 6.15 trials for relearning in contrast to 61.59 ± 8.05 of the second group. When measured by trials less correct runs the average relearning score of Group I is 20.83 ± 4.92 whereas that of Group II is 33.36 ± 6.49. In other words, the interpolative group made slightly over twice as many errors as the non-interpolated group, and required one-fourth more trials or roughly half more trials minus correct runs than the control group.

C. Correlation of the extent of lesion with learning and relearning. Table 8 shows the correlation values for our operated groups.

TABLE 8

CORRELATIONS BETWEEN EXTENT OF LESION AND ORIGINAL LEARNING OR RELEARNING AND INTERPOLATED LEARNING

		Oper. I	Oper. II
Correl. between ext. of lesion and learning of Orig. Maze A	1. Errors	0.16±0.02	0.65±0.08
	2. Errors	0.14±0.01	0.54±0.11
Correl. between ext. of lesion and relearning of Maze A	1. Errors	—0.12±0.15	0.65±0.08
	2. Trials	—0.08±0.15	0.69±0.08
Correl. between ext. of lesion and interp. learning on Maze B	1. Errors	———	0.49±0.11
	2. Trials	———	0.45±0.12

For Group I the correlation between extent of lesion and learning is low (0.16±0.02 in terms of errors) and that between extent of injury and relearning is negative. This is perhaps attributable to the small range of distribution of the lesions in this group rather than to any other factors. In the case of Group II where the amounts of lesions are more widely varied we find a correlation of 0.65±0.08 to both learning and relearning in terms of errors. For Operated Group II, the correlation between the extent of lesion and interpolated learning on Maze *B* is 0.49±0.11 in terms of errors. These values indicate that the learning and relearning records on the original maze as well as learning scores on the interpolated maze are directly influenced by the extent of cerebral lesions.

D. Total extent of cortical lesions in the two groups. A comparison of the composite diagrams of the total extent of lesions in the two groups, which have not been reproduced here, shows that the lesions cover a large part of the neocortex with the possible exception of the tips of the frontal and occipital poles. The archipallium was not involved. The total extent of lesion in Group I covers very much the same fields as that of Group II.

We have not taken into account the additional factor of subcortical lesions, although we have noted them in our reconstruction work. As Lashley has demonstrated that correction for sub-cortical involvements slightly raised the correlations with extent of injuries, our omission of such procedure certainly would not significantly affect any of our results and conclusions.

E. Comparison of errors made in the first trial of learning and relearning tests. The average errors made in the initial trial of learning on Maze *A* for the two operated groups are 20.87 and 26.77, a slight advantage in favor of the control group (Table 5). In relearning one animal of Group I (No. 7) made an initial error score of 42 which equals exactly half of the total group score. When this is excluded, Group II made an average score (3.23) of slightly less than twice the number of errors made by Group I (1.91) in the initial trial of relearning. However, the individual variabilities are too great in both cases to make any deductions reliable (Table 6).

F. Individuals unaffected by time or interpolated activity during retention. One striking fact in the case of operated animals is that in Group I where there is no interpolated learning none of the rats made perfect scores in relearning tests, whereas one animal of the test group (No. 30, with 14.3% lesion) showed perfect errorless score in retention in spite of the fact that this animal had been subject to interpolated activity before retest. The reason for this remains obscure (Table 7).

When the relearning scores for the initial trial of the two groups are compared, however, 7 rats of Group I made perfect scores in the first day of the relearning in contradistinction to 3 cases of Group II. On the other hand, 4 of the 6 rats in Group I which failed to learn Maze *A* during the 150 trials allotted succeeded in mastering the same maze during the relearning period. In contrast to this, only 2 of the other 6 cases in Group II that experienced similar failures in learning made successful records during the relearning interval. This gives evidence that more animals of the test group are affected by the interpolative decrement than the control group.

G. Summaries of results with the operated cases. 1. The average percentage of cerebral lesion in Group I (without interpolated learning) is 14.74 ± 0.71 as against 17.28 ± 1.02 of the test group (Group II). The difference of roughly two and a half percent of the cortical surface injured is nullified by the fact that the two groups made practically equal records in average errors in the learning of Maze *A* (279.65 vs. 277.86). The average trial scores made by Group II (100.4) are somewhat higher than Group I (95.82). As this difference is insignificant the assumption is made that the two

groups started out with about the same level of learning proficiency on Maze *A*.

2. A comparison of the relearning scores of the groups reveals that the group with interpolated learning made an average error score of roughly two and a half times that of the control group (66.38 vs. 27.32). The average trials of Group II show an excess of about one-fourth over those of Group I, whereas the ratio of trials less correct runs made by the interpolative group to those of the non-interpolative group is roughly 3:2.

3. Further analysis of the data tends to support the thesis that the retention values of the group subjected to interpolated activity of another maze are inferior to the group without such activity before retest.

3. *Comparison of Normal and Operated Cases.*

A. The effects of cerebral lesion upon original and interpolated learning. For an evaluation of the effects of cerebral lesions upon initial learning, we have four groups of animals for comparison, namely, two normal groups and two operated groups. In Table 9 the average learning scores of the four groups together with the average percentages of lesion of the operated groups are arranged.

TABLE 9

COMPARISON OF THE INITIAL LEARNING SCORES ON MAZE *A* OF THE NORMAL AND OPERATED CASES

The scores of the two normal groups are combined and averaged to be compared with those of the operated groups similarly treated.

			Average learning scores		
Group	No. of animals	Percent lesion	Errors	Trials	Trials less correct runs
Norm. I	25	0	71.96	49.2	21.04
Norm. II	25	0	71.84	49.2	20.16
Av. of 2 normal groups			71.9	49.2	20.6
Oper. I	23	14.74	279.65	95.82	56.74
Oper. II	22	17.28	277.86	100.4	65.73
Av. of 2 oper. groups		16.01	278.75	98.11	61.23
Oper. av. as percentage of norm. av.			387%	199%	297%

To facilitate comparison, the combined scores of the two normal groups are further averaged as are those of the two operated groups. The two normal groups together give an average learning score of 71.9 errors, whereas the two operated groups with an average lesion of 16.01 percent give 278.75 errors. The two operated groups thus made on the average 3.87, or practically four times as many errors as the two normal groups. The inferiority of initial learning ability of the operated animals as compared with the normals is obvious.

The two normal groups required an average of 49.2 trials whereas the two operated groups, including those cases which failed to reach the criterion during the allotted interval, required an average of 98.11 trials for learning the same maze, which is just about twice the former. In terms of trials minus errorless runs, the average for the two normal groups is 20.6 in contrast to 61.23 of the operated cases. Taking all the measures together, the operated animals made about four times as many errors as the normals, and required two to three times as much practice in terms of trials and trials less correct runs respectively as the normals. This is in accord with Lashley's results that his operated cases with an average of 31.1 percent lesion required six and one-half times as much practice as normals according to all measures.

On the interpolated Maze *B,* the operated group made about two and a third times the number of errors, required roughly twice as many trials and two and two-thirds times the number of trials minus correct runs as the normal animals trained in the same maze (Table 10).

TABLE 10

COMPARISON OF THE INTERPOLATED LEARNING SCORES IN NORMAL AND OPERATED CASES

	Learning scores on Maze B		
Group	Errors	Trials	Trials less correct runs
Norm. II	44.56	44.4	16.56
Oper. II	105.77	84.09	46.18
Oper. score as percentage of normal score	237%	188%	279%

B. The effects of cerebral lesions upon retentiveness with and without interpolated training. (*a*). *Absolute scores.* Table 11 shows the absolute scores in retention tests made by normal and

TABLE 11

COMPARISON OF RELEARNING SCORES OF NORMAL AND OPERATED CASES TRAINED UNDER PARALLEL CONDITIONS

Figures in parenthesis show the scores of the interpolated group expressed as percentages of the corresponding scores of the control group.

	Without interpolated training			With interpolated training		
Group	Errors	Trials	Trials minus correct runs	Errors	Trials	Trials minus correct runs
Normal	3.84	21.76	2.84	7.2	26.72	4.44
				(187)	(122)	(157)
Operated	27.32	49.61	20.83	66.38	61.59	33.36
				(242)	(124)	(161)
Oper. score as percentage of norm. score	711	228	733	922	230	751

operated animals with and without training on the second maze interpolated between original learning and retention tests. As in initial learning the operated animals are very seriously retarded in comparison with their normal controls.

Our major interest is in the question whether or not the interpolated training has a proportionately greater influence upon the retentiveness of the operated animals than of normal ones. We may make this comparison in several ways: by comparing the percentage differences in relearning scores between the operated animals and the normals trained under the same conditions; by determining the percentage increase in retention scores after interpolated training over the scores without interpolated training; by comparing the "savings scores" with and without interpolated training; and by comparing the scores of the groups on the first trial of the retention tests.

The third line in Table 11 gives the percentage scores of the operated animals in terms of the normals tested under the same conditions. For errors the interpolation of training increased the inferiority of the operated animals from 711 to 922 per cent of the normal scores. For trials and for trials minus correct runs the increase in percentage after interpolated training is scarcely significant. The average percentage inferiority of the operated group for the three criteria is for cases without interpolated training 591, for the cases with interpolated training 634. The difference here is very

small, as compared with the differences between normal and operated animals.

Comparing the scores of animals having interpolated training with their corresponding controls (figures in parenthesis in Table 11) we see that interpolated training raised the error score of normal animals from 3.8 to 7.2, an increase of 87 per cent. For operated animals this increase is 142 per cent. By the other criteria the difference between normal and operated groups is not significant. Thus in terms of retraining records, the interpolated learning produces a slightly greater effect in the error scores of operated than of normal animals, but has no significant effect upon the trial scores. Figure 6 shows the comparisons of learning and relearning scores of four groups of animals in terms of errors.

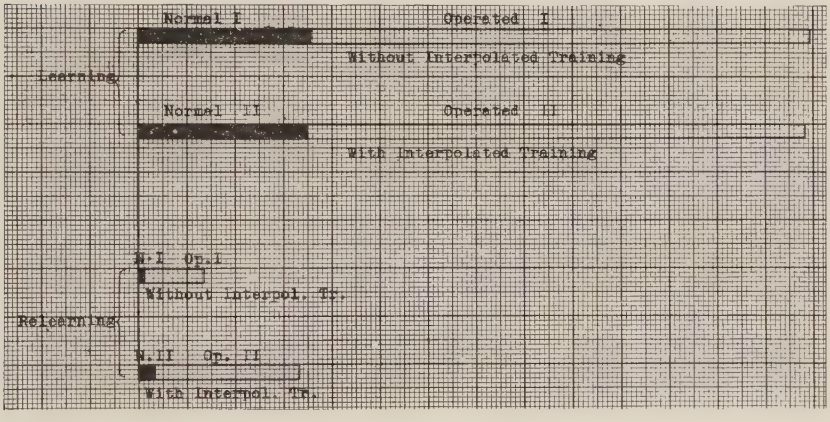

FIGURE 6

A Comparison of Learning and Relearning Scores of the Four Groups of Animals on Maze A in Terms of Errors

Score of the normal group is shown as shaded portion on the scale of its corresponding operated group.

(*b*). *Savings scores.* Individual savings scores have been computed for each animal according to the following formula:

$$\textit{Savings Score} = \left(100 - \frac{\textit{No. of Errors in Relearning}}{\textit{No. of Errors in Learning}} \times 100\right)$$

The mean savings scores of the four groups as computed from individual scores in terms of errors are given below:

Normal I	93.61±1.16
Normal II	88.52±1.72
Operated I	85.62±2.47
Operated II	74.68±7.13

With normal animals, therefore, the effect of interpolated training is to reduce the savings score by 5 per cent, with operated animals by 11 per cent.

(*c*). *Errors in first trial.* In the initial trial of the relearning tests Normal Group I made an average of 0.28 and Group II an average of 1.48 errors (Table 6). The difference here is 1.20 errors, or an increase of 428 per cent as a result of interpolated training. Operated Group I made an average of 1.91 errors on the first trial of retraining and Operated Group II an average of 3.23. The difference is 1.32, an increase of only 70 per cent as the result of interpolated training. Judged in terms of the scores for the first trial of retention tests the interpolated training produced a significantly greater loss in the normal than in the operated animals.

In terms of cases which made errorless scores on the first trial of retraining, the results favor the normal cases. For the four groups, the numbers of animals making errorless scores on the first trial were the following: Normal Group I, 16; Normal Group II, 12; Operated Group I, 7; Operated Group II, 3. The interpolated training apparently reduced the number of cases making errorless scores proportionately more among operated than among normal animals.

C. Conclusions concerning relative effects of interpolated activity upon retention in normal and operated animals. 1. By all criteria and methods of comparison the retention scores of the operated animals are very greatly inferior to those of their normal controls. The differences are statistically reliable and leave no doubt that animals which learn the maze after the destruction of cerebral tissue are markedly inferior to normal animals in their ability to traverse the maze after an interval of time.

2. The experiments have shown, further, that training upon a second maze, interpolated during the retention period, has a slightly

more deleterious effect upon retention in operated than in normal animals. The data here are, however, not consistent. In terms of the total error scores and the number of individuals making errorless runs on the first trial of retention tests, the operated animals with interpolated training are proportionately inferior to the normal ones. But the scores for trials show no significant difference between the normal and operated animals and the errors made on the first trial of retention tests indicate less effect of the interpolated training upon the operated than upon the normal animals.

4. *Relative Effectiveness of the Different Factors Contributive to Retention and Forgetting.*

A. Deterioration of the learned habit as due to the passage of time alone. Being the first experimenter to have measured the reduction of retention in man as due to the passage of time alone, Ebbinghaus discovered that the curve of retention for nonsense materials drops very rapidly during the first 20 minutes after learning and over half of the original material memorized is lost at the end of the first hour. Tsai, who made a systematic study on retention of motor habits in rats, found a deterioration of about 40 per cent of the old habit in a Carr maze 12 weeks after mastery. With the group of 25 normal rats trained on Maze *A* (Group I) we find that the average of individual savings scores after 40 days of no learning is 93.61 per cent. During the 40-day interval only slightly less than 7 per cent of the habit is lost. According to Tsai's data, one group of 12 animals tested six weeks after learning the Carr maze, which roughly correspond to our 40-day interval, shows a percentage of saving of only 79.65 in terms of errors (34, p. 15). Evidently our animals retained the habit much better than his cases. Aside from the difference in maze patterns used, Tsai adopted as criterion of learning only three consecutive trials without error as opposed to 10 successively correct trials in our case. Despite such differences the fact remains that very little of the maze habit is lost in rats after relatively long periods of retention.

B. Reduction in retention as due to time plus interpolated activity. Our Normal Group II is the one best fitted for testing out the additional factor of the interpolated activity of another maze upon retention over that of time alone. Taking the relearning scores of the control group as a norm we find that the test group made about 1.8 times more errors than the former. Assuming the

potency of time factor contributive to the reduction of memory as unity, then the relative valence of the additional interpolated activity would be roughly twice as much within limits of the present experiment.

C. Cerebral lesions as by far the most potent factor of memory retardation. Table 12 is so arranged as to show the relative degrees

TABLE 12

COMPARISON OF THE VARIOUS FACTORS RESPONSIBLE FOR THE RETARDATION IN RETENTION OF MAZE HABITS IN RATS AS TESTED BY THE EXPERIMENTS

	Reduction in retention as due to			
	Time (Norm. I)	Time + Interpolated activity (Norm. II)	Time + cerebral lesion (15%) (Oper. I)	Time + Interpolated activity + 17% lesion (Oper. II)
Percentage values with average relearning error score of normal I as standard	100	187.5	711.46	1728.65
Ratio	1	2	7	17

of effectiveness with which the factors of time, interpolated activity and cerebral lesions, either individually or collectively, act deleteriously upon retention as studied in these experiments. The average relearning value in errors of Normal Group I is used as a norm and those of the other groups are figured respectively as percentages thereof. In this way the relative amounts of reduction in retention as due to the factors studied can be compared and are expressed as ratios. Of course, such a comparison is suggestive rather than conclusive. But, within the limits studied in these experiments, it shows the preponderant importance of cerebral lesions as a factor in effecting memory retardation. The interpolated activity roughly doubles the error scores of relearning in both normal and operated cases, but the cerebral lesions (from an average of 15 to 17%) raise the errors scores to about 7 or 9 times the normal records.

Since there is some indication that the interpolated training may produce a slightly greater loss in operated than in normal animals we must ask whether the whole difference between the normal and operated animals can be ascribed to disintegrating effect of the intervening activity. Presumably the animals are learning other

things than the interpolated maze during the retention period and each of these may have some effect upon the original maze habit. However, studies of "retroactive inhibition" with human subjects show rather conclusively that this effect does not occur unless there is sufficient similarity between the original and interpolated material to introduce some confusion between the two situations.

During the retention period our animals were kept in small familiar cages. After learning the interpolated maze they were run daily on a straight runway, already familiar before initial training. They had no other opportunity for contact with a new environment. It is difficult to imagine any condition, short of complete anesthesia, offering less opportunity for the formation of conflicting habits. Except for the interpolated maze, there was certainly no opportunity for the formation of habits dealing with new special situations and this is the only type of activity for which there is any reason to expect a deteriorating effect upon the maze habit.

In view of the questionable evidence for any greater effect of interpolated training upon the operated animals, and the absence of opportunity for the formation of any other interfering habits during the retention period, we feel justified in concluding that the poorer retentiveness of the operated animals cannot be wholly ascribed to "retroactive inhibition" by activities during the retention period.

D. Comparison of Lashley's data with the present experimental results. Lashley subjected two groups of animals, an operated and a normal group, to learning an alternation maze (Maze III) and after 40 days in which they went through three successive stages of interpolated activities on different problems, he required his subjects to relearn the first maze (12). The number of animals employed in each of his two groups is very close to those of our groups. The maze adopted in his experiment, though similar in structure, is different from Maze *A* of the present experiment due to a positional shift of the entrance compartment. Nevertheless, it is still possible to make a direct comparison. His normal animals learned his Maze III quicker than my cases on Maze *A* as the former made an average error record of only 47 ± 2 as against roughly 72 of my groups. Moreover, it is important to note that his operated animals had far more extensive lesions than my cases, averaging 31.1 per cent as contrasted with about 16 per cent of my two groups. With these

salient differences in mind we shall attempt to compare Lashley's records with the present results which are represented graphically in the following diagram (Figure 7) drawn to the same scale. The

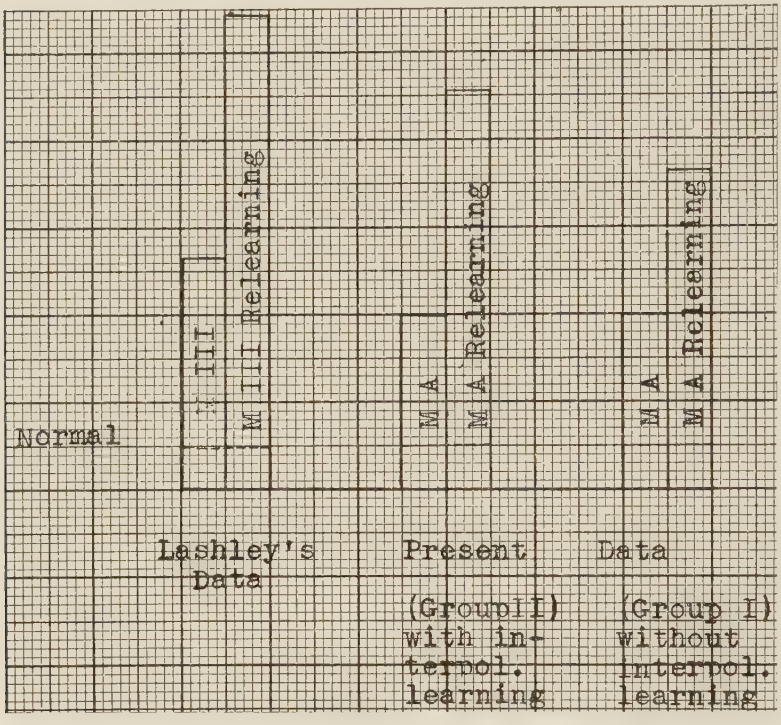

FIGURE 7

COMPARISON OF THE PRESENT DATA WITH DR. LASHLEY'S RESULTS ON LEARNING AND RELEARNING IN NORMAL AND OPERATED RATS

The average of operated animals is shown as percentage of the respective normal average, indicated by the dotted line marked "Normal." Our present data are based upon error scores. See Lashley's Monograph, p. 43.

average learning and relearning scores of animals in the operated cases are shown as percentages of the normal averages, indicated by the broken line. Irrespective of the disturbance caused by the interpolated training in all cases, there is a clear indication of a marked retardation in retention of the animals with brain injury.

In each case the defect in relearning is proportionately greater

than in initial learning, when compared with the scores of normal animals. The retardation in Lashley's series more closely resembles our group with interpolated training than that without, but it is doubtful whether the reliability of any of the figures is sufficient to justify a conclusion from this.

The fact that the relearning scores of operated animals are more seriously retarded than those of initial learning is evidence that the poor retention, measured by the savings method, is not merely an expression of reduced learning ability, but contains also an additional factor of poor retentiveness. This is borne out also by our data upon errors in the initial trial of relearning, in which the operated cases are significantly inferior to the normals.

IV. Discussion

The current theory of learning assumes a reduction of synaptic resistance in the conduction system as a basis for habit formation and memorization. If this theory is correct, then we should expect that animals with cerebral injury inflicted prior to learning a maze would show as much deterioration of the habit during a definite time interval after mastery of the problem as the normals, since the effacement of the synaptic changes in the nervous system should theoretically be nearly equal in operated as well as normal animals after the connections are once established. In contradiction to the expectations from this theory, our results show a disproportionately greater retardation in retention, as tested by relearning scores, in the operated cases than in normals trained under similar conditions. The relearning performances are even more seriously deteriorated in the operated animals than their initial learning efficiencies in proportion to the normal records. Taking the combined scores of the two normal groups as unity, the operated groups required three times as much practice for learning but required six times as much practice for relearning the same maze by all measures irrespective of interpolated training. This could be attributable only to a genuine reduction in retentiveness due to the cerebral lesions. Moreover, the significant correlation between the extent of lesion and relearning for Operated Group II (0.65 ± 0.08 for errors) tends to indicate a mass relationship between the amount of cortical tissue available and the retentive function. The greater the amount of functional

tissue left intact at the time of relearning the better is the habit retained.

In the interpolated learning activity, the operated group consumed a larger portion of the allotted 40-day interval and required two and a half times more effort in the interpolated maze than the parallel normal group according to all measures. On the basis of the synaptic theory, we should expect a proportionately greater loss of the first maze habit in the operated cases than the normals due to the interpolation of the second maze as compared with their respective controls, since theoretically, more and longer training in the interpolated activity, if effective at all, should be more detrimental in causing an effacement or disturbance of the memory traces of the first habit. But we find the normal group with interpolated training made nearly twice as many errors as the group without interpolation, whereas similarly the operated interpolative group made only slightly over twice as many errors as its control group. The degree of decrement due to the interpolated activity remains relatively constant, as it were, in normal as well as operated cases in spite of the fact that the operated animals devoted far more effort in the interpolated activity than the normals. The theory of specific connections of memory traces seems entirely untenable in the face of such facts. Our study tends to show that the relative effectiveness of the reinstatement of the original maze habit depends upon the successful manipulation of two mutually interfering reaction patterns, which in turn depends upon the quantity of cerebral mass remaining intact or available at the time of relearning. The perseveration of behavior shown in some operated cases due to more extensive lesions indicates a non-plasticity of habit reorganization and hence a greater difficulty to reinstate the reaction pattern relevant to the relearning situation.

It is of course dangerous to infer too much from the results obtained from the rat to that of man. But to assume, as did Jenkins and Dallenbach as well as McGeoch, that forgetting is solely due to the obliteration of the old memory traces by the new is certainly far-fetched and generalizes too much. The indication of our experimental work is that in animals with cerebral lesions the great loss of habits with passage of time cannot be accounted for in terms of the interference of intervening activities and that it is rather a function of the size of the cerebral lesion. This result is not con-

sistent with the theory that forgetting is solely due to the interference of habits.

V. Summary and General Conclusions

Four groups of animals were trained in these experiments, two normal and two operated groups. All the animals were trained on an 8 culs-de-sac Maze *A* to a criterion of 10 consecutive errorless trials or training was discontinued at the end of 151 trials in case they did not reach the criterion earlier. After 40 days retention period, all the animals were required to relearn the same maze to criterion. The procedure was identical in all cases except that animals in one of the normal and operated groups learned a second Carr maze during the retention period, whereas the normal and operated animals in the control groups traversed daily a straight runway for exercise and food during the interval. The normal groups comprised 25 animals in each group, whereas 23 of Operated Group I (without interpolated training) and 22 cases of Operated Group II (with interpolated learning) completed the series, making a total of 95 animals. Comparison of the initial learning scores of the two normal groups shows that they were equated in learning capacity, in so far as maze scores are an index of this. Similarly the two operated groups were practically equal in their initial learning scores, although far inferior to the normal ones in ability.

1. In retention tests, as in initial learning, the animals with cerebral lesions were markedly inferior to the normal controls. Their records in retraining tests range from 228 to 922 per cent of the comparable scores of the normal animals, as judged by different criteria.

2. Interpolated training on the second maze produced an additional loss of the habit to that resulting from the interval without training in all cases. The increase ranged from 22 per cent to 142 per cent, by the various criteria of total relearning.

3. The differences between the normal and operated groups with reference to the effects of interpolated training were relatively slight and inconsistent by different criteria. In terms of total errors in relearning, the operated group was proportionately more affected than the normal group. In terms of trials and of trials less errorless runs, there was no significant difference between the groups, and in terms of the immediate retention, as measured by errors in

the first trial of retention tests, the operated animals were less affected than the normals.

4. In terms of total error scores, which brought out the greatest differences in effects of interpolated training between the normal and operated groups, the effectiveness of the interpolated training amounted to a doubling of the error scores. By the same criterion, the difference between all normal and all operated animals amounted to more than a seven-fold increase in the error scores. The effect of interpolated training upon retentiveness is therefore markedly less than the effect of cerebral lesion. Since the animals had little opportunity for interfering activities apart from the training on the interpolated maze, it is argued that greater susceptibility to "retroactive inhibition" is inadequate to account for the greater part of the inferiority in retentiveness of animals with cerebral lesions.

5. The results of the present experiments establish the preponderant effectiveness of the factor of cerebral lesions in contributing to the function of retention or forgetting over those of time and interpolated activity. Arguments are advanced against the current theory of synaptic connections of memory traces in favor of the mass action of the cerebral cortex in retention as proposed by Lashley.

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